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CHRONOLOGICAL DEVELOPMENT OF BEHAVIOR IN THE BLIND MOLE RAT (*SPALAX EHRENBERGI*)

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ABSTRACT: The blind mole rat (*Spalax ehrenbergi*) is a potentially highly aggressive solitary, subterranean rodent. Data on growth and development of pups are lacking since it is difficult to raise pups in captivity and, until recently, the blind mole rat has never bred in captivity. In this study six litters were maintained in six large semi-natural set-ups. We describe for the first time the chronological development of behavior in the blind mole rat from day of birth until the young disperse and establish their own independent territories. The relatively short gestation period (34 days) and low birth mass (5-6 g) combined with the need to acquire all survival skills prior to dispersal, are probably correlated with the relatively lengthy development of the blind mole rat compared to Bathyergidae.

The blind mole rat (*Spalax ehrenbergi*) is a highly aggressive, solitary, subterranean rodent. These characteristics make it difficult to maintain and breed in the laboratory and most past attempts to breed this species in captivity have failed (Nevo, 1969; Shanas *et al*, 1995); the first successful attempt occurred only recently (Gazit, Shanas & Terkel, 1996). Consequently, little is known about growth and development of mole rat pups. The blind mole rat breeds once a year in the winter although recent evidence has shown that it also appears to have the potential for summer breeding (Shanas *et al*, 1995; Gottreich *et al*, 1995; Zuri and Terkel, 1996). Litter size ranges from 1-6 young (3-4 on average), weighing 5-6 gram each (Nevo, 1961). The pups are born naked and become covered with fur by the age of two weeks, when they also begin to move about the nest area.

The only aspect of behavioral ontogeny which has been studied in

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the blind mole rat is the transition from vocal to seismic communication in wild caught pups and its correlation with the shift from social to solitary life style (Rado, Wollberg & Terkel, 1991; Rado, Wollberg & Terkel, 1992).

The behavioral and physiological development of species of subterranean rodents of the family Bathyergidae, has been studied and widely reviewed by Bennett *et al* (1991). In contrast, little is known about the behavioral development of North and South American subterranean rodents since most studies have been based on post-mortem measurements. Andersen (1978), in particular, has described the development of the Pocket gopher (*Thomomys talpoides*).

In the present article we describe the behavioral development of the blind mole rat from the day of birth until the young disperse and establish their own independent territories. We particularly focus on the development of motor activity; establishment of separate food storage; sparring, and the increasing aggression between mother and young and among siblings associated with the transition from social to solitary life style.

METHOD

Subjects

Eleven mole rat pups (6 males, 5 females) from six litters were studied. Three of the litters were conceived and born in captivity during this study; one pregnant female was captured in the field and gave birth in the laboratory; and two mothers with 1-2 week old litters were caught in the field and brought to the laboratory. The study lasted for three breeding seasons, i.e. three years.

Procedure

Each of the six mothers and their litters were placed in a separate experimental set-up (Figure 1), comprising five transparent plastic cages (22x43x13 cm) interconnected by transparent Perspex tubes (total length of 9 m, 54 mm inner diameter, ca. the diameter of an adult mole rat body). Each cage contained damp soil 10-15 cm deep, enabling the mole rats to dig tunnels and block the borders of their territories. The wire mesh cage lids were covered with a clear Perspex sheet preventing air flow over the system while enabling observation of the events

within the cages. This set-up thus modeled a natural tunnel system, with separate functional chambers and completely closed to external air flow. Removable screw barriers inserted in the tubes, separated the system into two sections (Figure 1) but allowed free access to both sides by the small sized young while restricting the mother to one section.

Room temperature ranged between 25 ± 2°C in summer and 19 ± 3°C in winter, and lighting was provided by natural light from a window.

Animal care was designed to cause the least possible disturbance. Food and nesting material were introduced twice weekly into the cage not used by the mother for her nest and into one cage in the pup area. The food provided included fresh green grass and oxalis bulbs (*Oxalis cernua*) that comprise a large part of the mole rat's diet in nature, as well as apples, carrots, lettuce, sunflower seeds, and peanuts. The cages were cleaned at approximately ten day intervals, focusing predominantly on the toilet area.
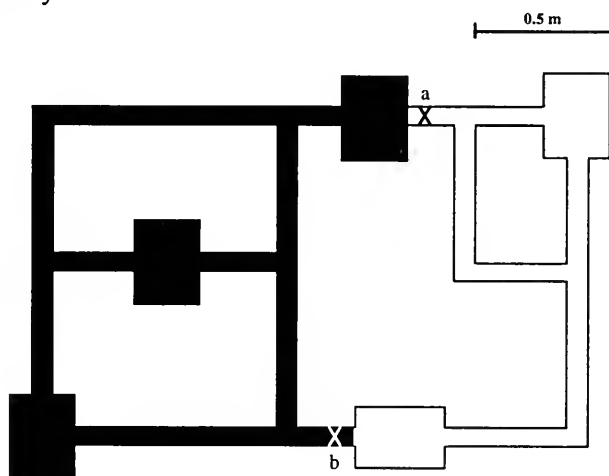
Figure 1. Schematic representation of the experimental set-up, showing the area available to the mother (black) who is too large to pass through the screw barriers (a,b), while the entire set-up (both areas - black and white) is available to the young.

Measures

Direct daily observations of each individual pup took place over 4-5 months, beginning on the day of birth or capture. Each observation lasted for two hours during the animal's active period.

In order to obtain a complete picture of the ontogeny of mole rat pups' behavior, twenty four different behavioral acts were recorded, in the chronological order in which they appeared. A brief description of the behaviors is presented in the results (see Table 1). In addition to the chronological development of behavior, detailed quantitative and qualitative data were collected from two siblings: male and female. Since it was impossible to perform such detailed observation on a larger number of pups, within the limits of this study, and based on previous observations in which we had found that there may be sex based differences in behaviors, the present study specifically selected a litter that contained one pup of each sex.

The types of functional categories of behavioral acts which we observed were: *Motor activity*; duration (in min) of pup activity throughout the observation period (excluding sleep); *Communication;* including chirps, jaw listening and head drumming, measured as number of events per time unit; *Play;* between pups (in min.) and *Interaction with mother or sibling;* either (a), when the two animals were in the same side of the set-up most of the interaction comprised playing or fighting or (b), when they were separated by the screw barrier the interaction comprised mainly building and dismantling the soil barrier, sniffing one another or gnawing at the screws.

RESULTS

Table 1 summarizes the chronological order of first appearance of each behavior pattern. By grouping the developing behavioral acts according to functional categories a more complete picture emerges of the progression toward adult behavior.

Motor activity

The pups began wandering around the nest at about two weeks. Until age 3-4 weeks, the mother would retrieve the pups to the nest by gently grasping almost any part of their body in her teeth. At six weeks the pups walked through the entire maternal tunnel system for the first time. The young mole rats usually walked with their noses in contact with the roof or floor of the tube. Reverse (backward) walking, used as frequently as forward walking by adult mole rats, first appeared at an age of five weeks on average; this behavior occurred even though the pups were still easily able to turn around inside the tubes and continue forward walking.

Table 1. Chronological appearance of behavior during development of mole rat pups.

Behaviors	Age	SE
Wandering out of nest into adjacent tube	14.5	0.2
Eating solid food in the nest area	20.7	2.3
Gathering food and carrying to mother's nest	31.3	4.4
Grooming head with forepaws	31.8	1.2
Backwards walking in tunnel	32.5	3.0
Use of maternal toilet for excrement	33.0	3.0
Scattered digging in soil in maternal cages	34.6	1.4
Jaw listening[1]	35.6	1.6
Play between pups	36.7	5.5
Wandering through the entire maternal tunnel	38.3	0.9
Teeth baring: exposure of incisors without biting	41.0	4.0
Weaning	44.0	2.0
Forming separate food storage from mother	45.4	5.4
Gathering nesting materials to mother's nest	49.5	8.3
Aggression between pups: teeth baring, biting, squeals	52.7	4.1
Head drumming[2]	56.5	5.3
Forming separate nest from mother	62.9	3.1
Aggression between mother and pups	64.5	5.1
Sleeping in separate nest during day	64.8	4.3
Sleeping in separate nest during night	66.4	14.9
Expulsion from maternal territory	70.3	4.6
Forming soil barrier at border with maternal territory	75.0	7.9
Duet head drumming between mother and pups	75.0	10.0
Urinating on soil barrier	102.0	24.0

[1] pressing lower jaw against tunnel wall to perceive vibrations
[2] the production of vibrations by tapping the head against tunnel ceiling

Food storage

During their first month, the pups spent almost all their time in the nest. The first three weeks were characterized by intensive maternal care, in which a significant portion of the mother's time was spent nursing the pups (Figure 2) and the mother stored food both in the nest area as well as in the food store. At 4-6 weeks, when the pups spent longer periods out of the nest, the female moved all the food items to the food store. At this stage the female began to seize food aggressively

from any pup that ate in the nest cage. At five to seven weeks, the pups began to gather and sort food items by type and arrange them in the mother's food store; and from seven weeks each pup began to create its own food store in the pup section of the set up. From age seven weeks until dispersal the pups gathered food for their own store as well as for their mother's. The frequency of food gathering to the mother's store was 0.3 ± 0.1 events and to the pups' store 2.8 ± 0.8 events, for 30 min. of observation (Mann Whitney U test, $p < 0.05$). Sex differences in food store location and formation were observed in three different litters: while forming their own food storage, the male pups stored only food items that were found in the pups' section, while female pups removed food items from the mother's food storage area into their own. This behavior stopped after two days when the mother became aggressive toward the female pups, which then ceased entering the mother's territory.
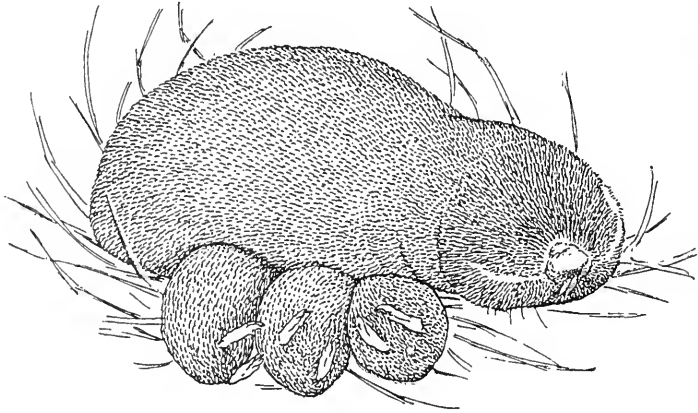
Figure 2. Female mole rat nursing her three pups. Drawing by Mr. W. Ferguson.

Play and Fighting

Play and fighting could be differentiated by several criteria: when playing the mole rats appeared relaxed and calm, their movements were gentle, smooth and slow, including gently locking their incisors, pulling and pushing each other and rolling together anterior - posteriorly. Play usually ceased suddenly when the mother approached or when the pups found a piece of food. The pups sometimes used their forefeet to push each other's head with one lying on its back and the other standing nearby. In nonaggressive play there were no bites or chirps.

In contrast, during fighting the animal's movements were quick and sharp, and accompanied by frequent short retreating jumps, often triggered by noise or movement in the vicinity. During fighting the mole rats primarily bit their opponent's body with their incisors and did not use their forefeet to push at each other, but stood on all four feet facing one another in a complete defense posture. Unlike play, the fights did not end suddenly as a result of exogenous stimuli such as nearby food; and during a serious fight it was difficult to separate the animals.

Sparring amongst pups began at six weeks and the aggression level (including bites, fights and chirps) gradually increased. At age 8-9 weeks most of the sibling interactions ended with fights and chirps. Since chirps are emitted by pups almost exclusively as a result of maternal or sibling aggression, the number of chirps emitted by the pups gave a good indication of the level of aggression. An increase in aggression was correlated with an increase in the number of chirps ($r^2 = 0.6$, $p = 0.0004$). Although the interaction length between pups did not change throughout maturation, the nature of the interaction changed to a more aggressive one at around age two months, as expressed by a sharp increase in chirps (Figure 3). Although aggression was frequent at this stage, most of the interactions between the pups did not develop into severe fights and eventually the pups went to sleep together in the mother's nest.
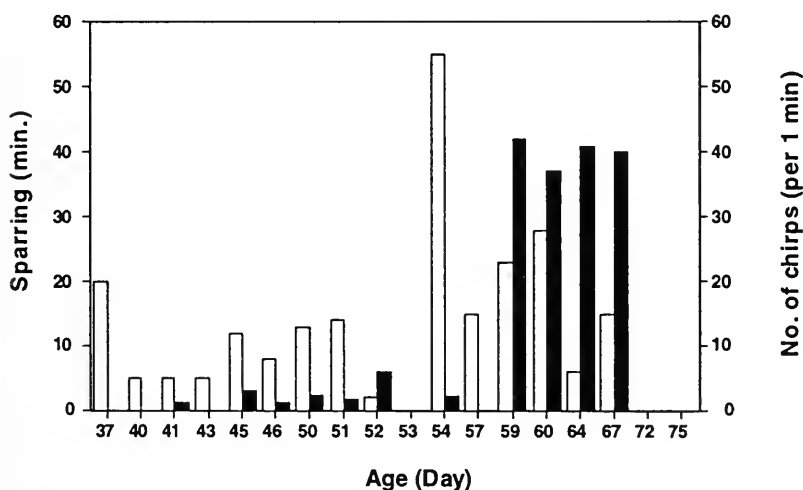
Figure 3. Duration of sparring between pups (white), and frequency of chirps (per min) emitted by the pups while sparring (black).

The presence of the mother played a major role in reducing the growing pups' aggression. As long as there was a possibility of physical contact between mother and young, aggression was suppressed. As soon as the young moved or were removed to separate territories, after reaching dispersal age, the full range of aggression was immediately expressed.

Mother - pup interaction

At the age of seven weeks, the mother started to play - fight with the pups: pushing, baring teeth and biting them gently. Although this interaction was characterized by fight elements it was of a playful nature since the pups remained calm and quiet and did not chirp or try to escape. These interactions gradually became more aggressive and the pups began to chirp more frequently when bitten by the female and frequently retreated to the nest or to the pup section of the apparatus.
During the establishment of the pup's independent territory, the interaction between mother and pup was characterized by mutual sniffing, gnawing at the screw barrier with their incisors, and pushing soil from one side of the barrier to the other. Throughout such interactions the pup chirped almost constantly.
The gender of the pup appeared to affect the total duration of interaction with its mother. Interactions between mother and male pup were significantly longer than between mother and female pup (Mann-Whitney U-test, $p < 0.01$). While the duration of interaction between mother and male pup increased after dispersal compared to before dispersal (Mann-Whitney U-test, $p < 0.01$), it decreased between mother and female pup after dispersal compared to before dispersal (Mann-Whitney U-test, $p < 0.05$) (Figure 4A). These interactions continued until the mole rats had formed a permanent soil barrier at the screw barrier area, separating the two territories. Following completion of the soil barrier, interactions decreased sharply and were limited to head drums and urination on the soil barrier.
Maternal aggression was expressed by attacking the pups with bared teeth and occasional bites, causing them to retreat to the nest while chirping. Throughout the entire period, maternal aggression was significantly higher toward the male compared to the female pup (Wilcoxon signed rank test, $p < 0.01$). From the age of eight to nine weeks, the male pup chirped every time the mother approached even when there was no physical contact between them. The female pup voiced fewer chirps than the male for the entire period. The frequency of vocalization decreased after dispersal for both the male (Mann-

Whitney U test, $p < 0.001$) and the female (Mann-Whitney U test, $p < 0.001$) (Figure 4B). After dispersal, when there was no physical contact between mother and pups, the pups' earlier high, sharp and loud chirps of fear were replaced by more drawn out, calmer chirps.
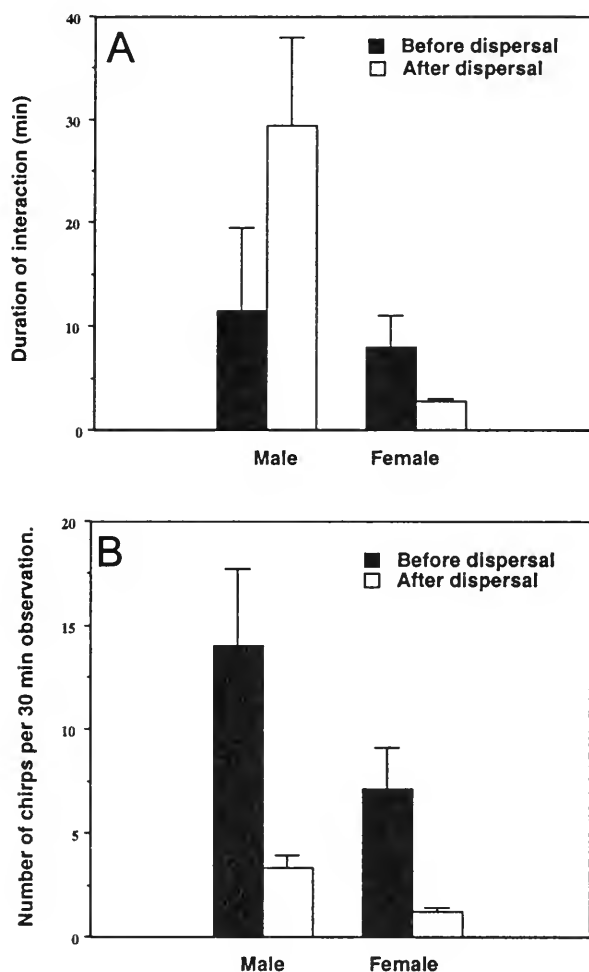
Figure 4. Interaction between mother and pups, when both resided in the mother's territory (black bars) or when the pups remained in their own territory (white bars) and were separated from their mother by the screw barrier. A, Duration of interaction (mins) between mother and pups and B, Number of chirps emitted by the pups during interactions with the mother.

Digging and establishment of a separate territory

Digging activity appeared very early in life, immediately after the appearance of vital behaviors such as independent eating and walking. At around five to six weeks the pups began to dig indiscriminately inside the mother's territory cages; while at eight weeks they were already digging straight tunnels inside the cages and pushing soil in the tube partitions.

The pups' exploration and use of the separate tunnel system adjacent to the mother's territory was gradual. At the beginning the pup blocked most of the available tubes with soil, using only a small part of the adjacent tunnel system. During the first week of territory establishment, the pups remained mainly in their own section, briefly returning to the mother's territory every 1-5 min. They gradually extended the time spent in the adjacent tunnel system, although still feeding from the mother's food storage and sleeping in the mother's nest. At the age of 11-12 weeks the pups dismantled the soil barrier that restricted the new territory length, and began to use the entire available tunnel. The young mole rats fully dispersed from the maternal territory at age 12 weeks (Figure 5).
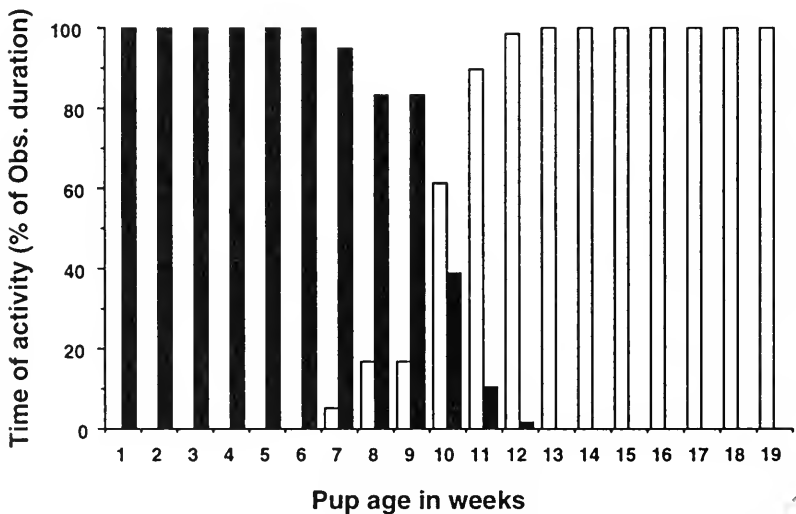
Figure 5. Percent of observation period that the male pup was present in the maternal territory (black) and in the separate territory (white).

The experimental apparatus used in our study had space for only one separate territory in addition to the mother's. In each of the five cases where there were opposite sex siblings, the male pup established his independent territory in the separate area. The female pup remained in the mother's territory for several weeks longer until a third section was added to the apparatus, or she was removed due to excessive maternal aggression.

During the establishment of their separate territories, when the pups returned to the mother's territory they pushed a small amount of soil onto the screw barrier separating the two territories. This behavior was observed 8 times for the male and 11 times for the female pups.

Elements of nest construction first appeared in four to five week old pups when they repaired the mother's nest. Approximately three weeks later, each pup began to build its own nest inside the maternal territory. At age 9-10 weeks, the male pup formed its own nest in the adjacent tunnel system, and one to two weeks later he was fully independent and rarely returned to the mother's nest.

Vocal and seismic communication

Detection of vibrations by jaw listening behavior was first performed at age five to six weeks, whereas the production of vibrations by head drumming was first performed only at age eight to nine weeks.

Head drumming increased significantly throughout the dispersal process of the pups; mean frequency of pup head drums in the maternal territory was 1 ± 0.4, compared to 6 ± 1.3 in the adjacent tunnel system, (per 30 min. of observation, Mann Whitney U test, $p < 0.01$). The same pattern also occurred with jaw listening; frequency of jaw listening performed by the pups in the maternal section was 2.2 ± 0.4 , while in the pup section it increased to 8 ± 1.3 (for 30 min of observation, Mann Whitney U test, $p = 0.01$).

Duets of head drumming between siblings or between pup and mother occurred only when the two animals were separated by the screw barrier. Most of the duets occurred between mother and male pup, although occasionally we observed a trio between mother, male pup and female pup.

DISCUSSION

The seasonal semi-arid climate in Israel poses some challenges to the subterranean life of the blind mole rat. The young mole rat must be

able to dig and establish its own tunnel system, defend it against intruders and gather an adequate amount of food items during the short period between establishing independence in the spring and the summer when the soil is dry and digging is difficult. Consequently, the young mole rat is selected to disperse from the maternal territory only when it is physically and behaviorally fully developed. The short gestation period (Gazit *et al,* 1996) and low birth weight (Nevo, 1961) of the blind mole rat compared to other solitary subterranean rodent species (Jarvis, 1969; Bennett & Jarvis, 1988; Bennett *et al,*1991; Jarvis & Bennett, 1991) except the pocket gopher (Andersen, 1978), are compensated for by the proportionally longer period of behavioral development from altricial infancy to independent maturity. During this developmental period, the young acquire strength and performance skills vital for survival.

The young of social species of mole rats (family Bathyergidae) which remain in the maternal tunnel system and are incorporated into the colony, benefit from the co-operative foraging activities of adults in the colony. Thus, the selection pressures acting on them are probably different from those acting on solitary mole rats (Bennett *et al,* 1991).

The need to establish an independent territory and to defend it against intruders is correlated with the development of aggression before the young disperse from the maternal territory. Sparring between pups, beginning at age 5-6 weeks, is the first stage of practice fighting. Although the differences between play and fighting are clear, both are characterized by many of the same elements of behavior, albeit more gentle during play. Gradually, aggression between pups increases until real fights begin at age 7-8 weeks, as occurs in all solitary genera of the family Bathyergidae (Bennett *et al,* 1991) and the pocket gopher (*Thomomys talpoides*) (Andersen, 1978). During the next period of 4-5 weeks, while still in the maternal territory, the pups practice the required skills for independent life including tunnel digging and repair, food gathering, nest construction and the use of seismic communication. These skills are applied afterwards when the pup begins to establish its own territory. Maternal aggression, which begins at 9-10 weeks, increases gradually parallel to the pup's establishment of independent territory and probably triggers the dispersal from the maternal territory at an age of 11-12 week almost a month later than within the solitary genera of Bathyergidae (Bennett & Jarvis, 1988; Bennett *et al,* 1991).

One dispersal strategy to prevent inbreeding is for the male to establish its territory far from the maternal and female sibling

territories. It is possible that the higher maternal aggression exhibited toward the male pups encourages them to disperse earlier than female pups, as was shown in the present study, and also to establish their territories at a greater distance. In the present study, after the pups have established their territories adjacent to the maternal territory, the duration of continued interaction between mother and male pup was significantly longer than with female pup, although before dispersal, the duration of interaction with both was almost the same. These post-dispersal interactions are aggressive and might encourage the male to keep away from the territories of female relatives. Rado *et al,* (1992) found that males dig long, straight tunnels directly away from the maternal territory, and suggest that this method of male dispersal may prevent potential inbreeding and conforms to the strategy of many other mammals in which dispersal of males usually takes place at greater distances than that of females (Greenwood, 1980).

Although the adult blind mole rat is highly solitary and aggressive, maternal and sibling aggression is strongly reduced during the rearing period. Such a mechanism is essential for the pups to complete physical and behavioral development prior to dispersal. As long as the mother is in the vicinity of the pups, sibling aggression is suppressed, and fully emerges only immediately after separation from the mother. Under certain specific environmental and social conditions there appears to be some flexibility in the time of onset of aggression. For instance, during severe winter flooding, the pups remain restricted to the nest with their mother for a prolonged period. In this case, both the initiation of aggression and of dispersal are delayed (Zuri and Terkel, 1998).

Since aggression between adult mole rats often ends in the serious injury or death of one or both animals, and since the reproductive fitness of the mother increases as more pups survive, it seems reasonable for aggression between siblings to be inhibited as long as the pups remain within the social structure of the maternal tunnel system. However, once the young leave the maternal territory and establish and maintain their own territory, aggression becomes an essential behavior to deter intruders, including relatives. This argument supports the sharp increase in aggression exhibited by the pups immediately after separation from the maternal territory.

The first reported case of breeding the blind mole rat in captivity occurred between a mother and son which inhabited the same apparatus for several months (Gazit *et al,* 1996). It is our belief that the maintenance of the male pup with its mother in the original apparatus contributed to the successful reproduction in captivity by reducing the

animal's aggression. A similar success in reproduction of the solitary species *Georychus capensis* occurred when a mother mated with her male pup after a long period of cohabitation (Bennett & Jarvis, 1988).

The temporal correlation between the pups' establishment of separate nest and food store and their increased aggressive interactions might reflect the beginning of competition among pups over occupation of the adjacent tunnel system, nest materials and food items. Evidence for sibling competition has also been found in nature (Rado *et al,* 1992). During the summer, the dry soil becomes hard to excavate and a mole rat that has not completed digging its tunnel system and gathering food during the wet season will bear a severe energetic disadvantage. The mother, having spent most of her energy rearing the young, must at the same time also collect sufficient food items to ensure her own survival through the long summer. The significance of food storage, therefore, is crucial for the mother as well as for the young. The mother's tolerance of the female pup's removal of food from her store is mystifying as it decreases her own chances of survival. Although this behavior could provide a significant advantage to the young female, it is unclear why it is restricted exclusively to female pups, since to all appearances both female and male pups face the same obstacles of survival. These gender differences of behavior might be derived from the different dispersal pattern between males and females, under which the female pups establish their territories adjacent to the mother's territory, while the males establish their territories at a greater distance.

The advantage of the vibrational channel of communication used by the blind mole rat is that vibrations carry long distances through soil, making this mode of communication effective between animals in two separate territories (Rado *et al,* 1991; Zuri and Terkel, 1996); while the vocal channel of communication is used only as long as the mother and young stay in the same tunnel system. The young mole rat begins to be aware of the surrounding vibrations by jaw listening earlier than it starts to produce these vibrations itself. While still in the maternal territory, the ability to detect vibrations in the environment is vital in order to avoid intruders or predators. Producing vibrations at this stage is still not necessary for survival, but becomes significant later when digging new tunnels. In the present study we found that the young mole rat performs jaw listening and head drumming behaviors significantly more frequently in its own new tunnel than in the maternal territory. Since it depends on creating and receiving vibrations in order to sense its environment, jaw listening and head drumming behaviors are thus more necessary, and performed by the young more frequently, in its

new unfamiliar tunnels than in the well-known maternal territory. The use of drumming signals while still linked to the maternal tunnel enables the young to discern its neighbors' territories and direction of digging, as suggested by Rado *et al,* (1992), and later confirmed after monitoring mole rats in nature (Zuri and Terkel, 1996).

Use of the vibrational mode of communication by hind foot drumming for territorial advertisement has been described for solitary species of the family Bathyergidae *(Bathyergus suillus, B. janetta, Georychus capensis)*, for the Rhyzomid *Tachyoryctes splendens* and for species of the Ctenomyidae and Geomyidae (Bennett and Jarvis, 1988; Bennett *et al,* 1991; Burda *et al,* 1990; Jarvis and Bennett, 1991; Narins *et al,* 1992). In most species, the use of seismic communication is initiated just prior to dispersal, except for species of the genus Bathyergus which first perform hind foot drumming 2-3 weeks after dispersal (Bennett *et al,* 1991), and thus probably do not use it to discern tunnel digging direction as in the blind mole rat.

In summary, the present study describes the gradual transition of the blind mole rat from altricial social infancy toward fully developed solitary maturity. Throughout the long developmental process the young channels its energy into growth and acquisition of skills such as digging, nest construction, food gathering, practice of vocal and seismic communication, and of aggressive behavior, all of which are vital for independent survival.   :

ACKNOWLEDGEMENTS

REFERENCES

Andersen, D.C. (1978). Observations on reproduction, growth, and behavior of the northern pocket gopher *(Thomomys talpoides)*. *Journal of Mammalogy, 59,* 418-422.

Bennett, N.C., & Jarvis, J.U.M. (1988). The reproductive biology of the Cape mole-rat, *Georychus capensis* (Rodentia, Bathyergidae). *Journal of Zoology, London, 214,* 95-106.

Bennett, N.C., Jarvis, J.U.M., Aguilar, G.H., & McDaid, E.J. (1991). Growth and development in six species of African mole-rats *(Rodentia: Bathyergidae). Journal of Zoology, London, 225,* 13-26.

Burda, H., Bruns, V., & Muller, M. (1990). Sensory adaptations in subterranean mammals. In E. Nevo (Ed.) *Evolution of subterranean mammals at the organismal and molecular levels* (pp. 269-294). Wiley-Liss: New York.

Gazit, I., Shanas, U., & Terkel, J. (1996). First successful breeding of the blind mole rat (*Spalax ehrenbergi*) in captivity. *Israel Journal of Zoology, 42,* 3-13.

Gottreich, A., Hammel, I., Yogev, L., & Terkel, J. (1995). Quantitative microscopic changes in the mole rat testes during an annual cycle. *Anatomical Record, 243,* 195-199.

Greenwood, P.J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour, 28,* 1140-1162.

Jarvis, J.U.M. (1969). Some aspects of the biology of East African mole rats. Ph.D. thesis, University of East Africa, Nairobi. In N.C. Bennett, J.U.M. Jarvis, Aguilar, G.H., & McDaid, E.J. (1991). Growth and development in six species of African mole-rats (*Rodentia: Bathyergidae*). *Journal of Zoology, London, 225,* 13-26.

Jarvis, J.U.M., & Bennett, N.C. (1991). Ecology and behavior of the family Bathyergidae. In P.W., Sherman, J.U.M. Jarvis, & R.D. Alexander (Eds.) *The biology of the naked mole-rat* (pp. 66-96). Princeton New Jersey: Princeton University Press.

Narins, P.M., Reichman, O.J., Jarvis, J.U.M., & Lewis, E.R. (1992). Seismic signal transmission between burrows of the Cape mole rat, *Georychus capensis. Journal of Comparative Physiology, 170,* 13-21.

Nevo, E. (1961). Observations on Israeli populations of the mole rat *Spalax e. ehrenbergi,* Nehring 1898. *Mammalia, 25,* 127-144.

Nevo, E. (1969). Mole Rat *Spalax ehrenbergi*: Mating behavior and its evolutionary significance. *Science. 163,* 484-486.

Rado, R., Wollberg, Z., & Terkel, J. (1991). The ontogeny of seismic communication during dispersal in the blind mole rat. *Animal Behaviour, 42,* 15-21.

Rado, R., Wollberg, Z., & Terkel, J. (1992). Dispersal of young mole rats (*Spalax ehrenbergi*) from the natal burrow. *Journal of Mammology, 73,* 885-890.

Shanas, U., Heth, G., Nevo, E., Shalgi, R., & Terkel, J. (1995). Reproductive behaviour in the female blind mole rat (*Spalax ehrenbergi*). *Journal of Zoology, London, 237,* 195-210.

Zuri, I., & Terkel, J. (1996). locomotor patterns, territory, and tunnel utilization in the mole rat *Spalax ehrenbergi. Journal of Zoology, London, 240,* 123-140.

Zuri, I., & Terkel, J. (1998). Ontogeny of agonistic behaviour in dispersing blind mole rats (*Spalax ehrenbergi*). *Aggressive Behaviour, 24 (6),* 455-470.

HOW MANY DIMENSIONS ARE NEEDED TO DESCRIBE TEMPERAMENT IN ANIMALS: A FACTOR REANALYSIS OF TWO DATA SETS

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ABSTRACT: Factor analysis has commonly been used to infer the dimensions of animal temperament. However, the results were often complicated by large number of broad and situation-specific factors caused by low psychometric adequacy of the correlation matrices, undermining the assumptions of factor analysis. In this study I reanalyzed the data sets obtained by Royce, Poley & Yeudall (1973) and Gervai & Csányi (1985) including, however, only the variables with high correlations (multiple $R^2 > 0.3$) and psychometric adequacies (Kaiser-Meyer-Olkin measure > 0.5). This yielded more stable and simpler factor solutions than in the original studies. Specifically, even though the present reanalysis cannot rule out the existence of other temperament factors, it indicates that two general dimensions, Activity-Exploration and Fear-Avoidance, are present in such diverse species as mice and the paradise fish.

Individual differences in behavior are well known to everyone who works with animals of virtually any species. Some of the recent reviews (Budaev, 1997a,b; Clark & Ehlinger, 1987; Eysenck & Eysenck, 1985; Stevenson-Hinde, 1983; Wilson, Clark, Coleman & Dearstyne, 1994) emphasized the importance of studying integrated behavioral phenotypes and stable traits that are consistent over time and across situations, that is, temperaments and personalities. Within such a framework human and animal temperament is viewed as a system of stable dimensions which are directly unobservable and must be inferred form the observed behavior in various situations.

The problem of extracting general temperamental traits is closely linked to geometrical models in which individuals are represented as points or vectors in a multidimensional space. The principal

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methodological task here is to find some solution with a minimum number of most salient temperament dimensions. It is performed typically by means of factor analysis. Because a few general factors can account for a large number of variables, the application of factor analysis brings interpretability and parsimony into the data.

The current evidence indicates that two broad dimensions, namely, Activity-Exploration (incorporating such traits as exploration, stimulus-seeking propensity and sociability) and Fear-Avoidance (composed of shyness, fearfulness, anxiety and escape propensity) were systematically observed in various vertebrate species. This implies that common adaptive, neural and hormonal mechanisms may be involved (Royce, 1977; Budaev, 1997a,b). For example, it is tempting to suppose (Budaev, 1997a,b) that in humans the dimensions analogous to Approach and Fear-Avoidance may represent two major personality dimensions, Extraversion-Introversion and Neuroticism, which are known to have clear physiological background and high heritability.

However, the results of most analyses turned out to be often complicated, and in addition to these two factors involved additional ones lacking replicability (to note only a few references: Cattell & Korth, 1973 in dogs, Royce, Poley & Yeudall, 1973 in mice; Gerlai & Csányi, 1990 in fish; Cattell, 1973 in humans). This was, probably, because many of these studies were conducted to take as many different variables as possible sampled as widely as possible, to cover the whole "personality sphere" (see Cattell, 1973). In this tradition "only a few variables can ever justifiably be eliminated, and the need for this elimination must be strong" (Cattell & Korth, 1973, p. 17), even though one can potentially measure a literally infinite number of behavioral variables. A methodological criticism often arises, namely, that factoring an arbitrary collection of heterogeneous variables with the primary aim to "invent hypotheses" in some inductive way, is methodologically flawed (e.g. Eysenck & Eysenck, 1985). But in many exploratory studies there may simply be no feasible alternative and a potentially important facet of temperament can be overlooked if some variables are arbitrarily omitted.

However, a more serious problem with such sparse analyses is of a statistical nature. The "personality sphere" approach has been criticized on the ground that correlations between diverse, randomly sampled variables approach correlations between random deviates (Humphreys et al, 1969). The issue of simultaneous statistical inference (note that the number of individual correlations is proportional to the square of the number of variables in the matrix) is also obvious. Computing a

collection of multiple tests based on a particular fixed overall significance level results in a high probability that some tests are significant by chance alone (Wright, 1992). Furthermore, excessive error variance could inflate communalities and produce spurious factors (Armstrong & Soelberg, 1968; Horn, 1967). As Armstrong & Soelberg (1968) demonstrated, an ostensibly interpretable factor pattern matrix may be obtained through application of the principal component analysis to even a collection random normal deviates.

Many analyses can also suffer from inappropriate statistical analysis. As Zwick and Velicer's (1986) examination has shown, the most widespread rule of thumb to retain as many factors as their eigenvalues exceed unity, is extremely poor and "very likely to provide a grossly wrong answer", which "seems to guarantee that a large number of incorrect findings will continue to be reported" (p. 439). In fact, the Kaiser's root-one method often overestimates the number of factors (Revelle & Rocklin, 1979; Zwick & Velicer, 1986), and a few broad factors are typically found more replicable across studies than many narrow factors (e.g. Guilford, 1977; Saville & Blinkhorn, 1981). Thus, some of the previously defined numerous factors of temperament in animals may be entirely spurious.

A detailed examination and reanalysis is possible for the data sets obtained by Royce, Poley & Yeudall (1973) and Gervai & Csányi (1985), in which the raw correlation matrices are available. An additional advantage is that both are based on unusually large sample sizes (respectively 775 mice *Mus musculus*, and 120 paradise fish *Macropodus opercularis*). Yet, a closer inspection reveals that in both cases some definitely spurious factors were interpreted. In the original study of Royce *et al* one can find at least two clear examples. The factor 13 was identified by two variables, however, at the neighboring page (Table 1, p. 40) one sees that these variables were surely uncorrelated ($r = -0.043$; $p > 0.1$ unadjusted for multiple tests); another example is the factor 15, also composed of equally unrelated variables. The factors containing one or more variables which do not correlate significantly (without adjustment for multiple inference) with other variables may also be found in the principal component solution of Gervai & Csányi (1985).

The aim of the present investigation was to reanalyze the correlation matrices of Royce, Poley & Yeudall (1973) and Gervai & Csányi (1985). Reanalysis of the existing data set provides a significant advantage over a collection of new data. One can hypothesize (see above) that two relatively independent factors would appear in both

cases, although of course additional factors cannot be ruled out. The measures of exploratory behavior and activity would correlate together and form the Activity-Exploration dimension whereas the measures of fearfulness would make up the Fear-Avoidance factor. This reanalysis is also interesting because neither Royce *et al* (1973) nor Gervai & Csányi (1985) hypothesized any structure, and variable selection was fully agnostic.

METHOD

The behavioral tests and measures are described in the original studies of Royce *et al* (1973) and Gervai & Csányi (1985), so only a brief account is provided here. Royce *et al* (1973) tested 775 mice of several strains in 12 tests presumed to measure their emotionality. Forty two variables were recorded in total including: avoidance conditioning, individual emergence and removal from a small cylindrical cage, activity wheels, open field test, straightway, platform on an elevated pole, emergence from dark into light and from light into dark, food goal-box test, circular activity with and without bell, and underwater swimming. Gervai and Csányi (1985) tested 120 paradise fish of three strains in three tests (restricted novel environment, approach to a novel object, emergence from a shelter and open field test). Unlike Royce *et al* (1973), who recorded arbitrary behavioral measures in the tests, Gervai and Csányi (1985) recorded elements of the natural ethogram of the paradise fish including; freezing, escape, air-gulping, moving, creeping, and approaching a novel object (this allows a direct quantitative comparison of temperament factors in the paradise fish with those identified in the guppy *Poecilia reticulata*, Budaev, 1997b). Both Royce *et al* (1973) and Gervai and Csányi (1985) factor-analyzed total correlation matrices, with all strains collapsed. For continuity, the same nomenclature as in the original papers is used for the behavioral measures.

The correlation matrices presented in the papers of Royce *et al* (1973) and Gervai and Csányi (1985) were entered into a computer and checked for errors. To estimate the degree to which components of the correlation matrix shared common variance, the Bartlett's sphericity test and the overall Kaiser-Meyer-Olkin measure of sampling adequacy (KMO) were computed and the off-diagonal elements of the anti-image covariance matrix (Dziuban & Shirkey, 1974) were examined. Separate KMO indices were computed for each variable to assess their individual

factoring adequacy. Computation of the KMO index is desirable because a particular variable may have a high correlation with another variable, but still have poor adequacy, grossly falling out of the general pattern (e.g. if this is a chance correlation). Variables with KMO < 0.5 are likely to impair the factor solution and should be removed; no meaningful factors can be extracted if the overall value of KMO is smaller then about 0.5 since the correlation matrix approaches a random matrix (see Dziuban & Shirkey, 1974).

To identify unique uncorrelated variables, values of the squared multiple correlation coefficient (R^2) were examined for each variable. Then, the KMO indices for each variable were computed and those with KMO < 0.5 were excluded. The resulting subsets of variables were subjected to the final factor analysis. The multiple R^2 were used as initial estimates of communalities. The MINRES approach (in which the initial estimates of factor loadings are adjusted iteratively to minimize the residual sum of squares) was used for factor extraction, and the factor pattern matrix was rotated according to the normalized Varimax criterion (Wherry, 1984). Several other methods of extraction and rotation were also tried which yielded virtually identical results. To assess the number of factors inherent in the data, four different tests were employed: the Cattell's scree-plot, the Kaiser's rule to retain only factors with eigenvalues greater than unity (Wherry, 1984), the Revelle & Rocklin's (1979) Very Simple Structure (VSS) method, and the approach based on parallel analysis of simulated data (PA, see Zwick & Velicer, 1986), involving 100 random samples in each case. The tests showed no gross discrepancies.

Finally, a direct comparison of temperament factors identified in the paradise fish in the data of Gervai & Csányi (1985) with those determined in the guppy in a recent study (see Budaev, 1997b) was performed. Ahmavaara (Wherry, 1984), Tucker, Pearson and Kaiser-Hunka-Bianchini (KHB) factor comparison coefficients were computed for particular pairs of factors, as well as the KHB mean solution cosine for the overall agreement (Barrett, 1986). It was desirable to compute several independent indices based on different underlying assumptions (see Barrett, 1986).

RESULTS

The overall level of absolute off-diagonal correlation coefficients within the matrix of Royce *et al* (1973) was very low (very high

proportion of essentially zero correlations), possibly caused by low ecological validity of the arbitrary behavioral variables. In contrast, the correlations within the matrix of Gervai and Csányi (1985) were distributed bimodally with a good proportion of nonzero correlations (note that variables were represented by elements of the natural species' ethogram). The distribution of the multiple correlation coefficients in both cases was multi-modal (Figure 1) making it possible to establish a reasonable cut-off value for discarding poorly correlated variables. In the data of Royce *et al* (1973) it was 0.3 (the first gap, see Figure 1) while in the dat of Gervai and Csányi (1985), it was 0.5.

While having relatively large multiple R^2 values (0.4-0.7), the four variables of weight at 40, 62 and 67 days (1, 35, 42) and sex (2), were also excluded from the final analysis of the data of Royce *et al* (1973). This was because they formed a separate well-defined factor (without salient loadings by the behavioral measures) and were considered of not much importance theoretically (see Cattell & Korth, 1973 for a similar

Royce, Poley & Yeudal (1973)   Gervai & Csányi (1985)
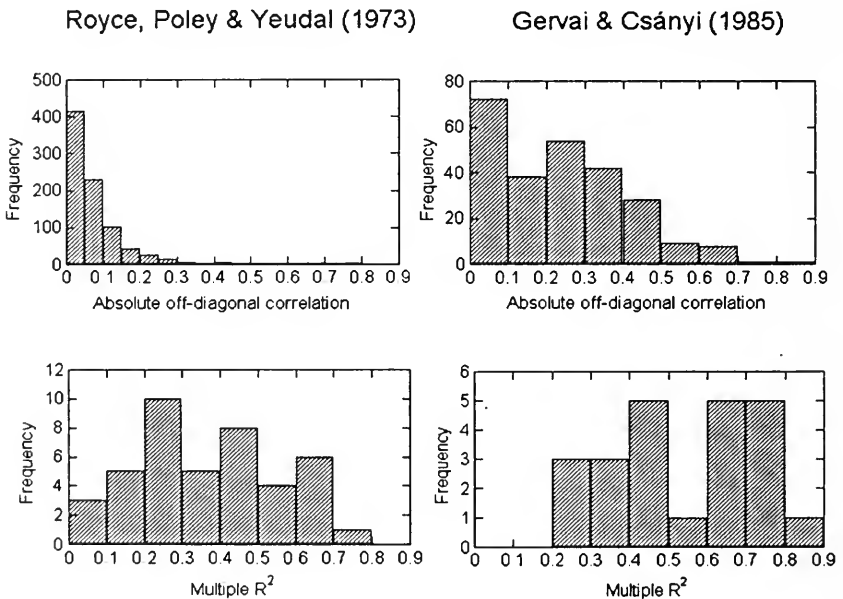
Figure 1. The analysis of the correlation matrices. Upper row, the distribution of individual correlation coefficients within the correlation matrices of Royce *et al* (1973) (left) and Gervai & Csányi (1985) (right). Lower row, the distribution of multiple correlation coefficients (squared values) in the data sets of Royce *et al* (left) and Gervai & Csányi (right).

unitary "body size" factor in dogs, and Budaev, 1997b for a report of no relation between temperament and size in a fish). However, the measures of sampling adequacy were computed including as well as excluding these variables.

As Table 1 shows, in both Royce *et al* (1973) and Gervai and Csányi (1985) data sets, the procedure of variable reduction led to an improvement of the overall KMO measures of sampling adequacy. Not surprisingly, exclusion of the well-identified factor containing weight and sex variables reduced it in the data of Royce *et al* (1973). Other measures of sampling adequacy (Table 1) revealed similar results, although in the Royce *et al* (1973) data the proportion of nonzero anti-image covariances increased. Thus, the reduced correlation matrices were more appropriate for factoring.

Table 1. Effect of the exclusion of variables on the measures of sampling adequacy. Data set of Royce *et al* analysed A, with and B, without the weight and sex variables; df, equivalent to the number of correlations in the Bartlett's test; χ^2, from Bartlett's sphericity test, $p < 0.001$ for all values; KMO, Kaiser-Meyer-Olkin measure; %, percentage off-diagonal anti-image covariances > 0.09.

	Data set analysed		df	χ^2	KMO	%
Complete Matrix	Royce, Poley & Yeudall (1973)	A	861	9051	0.62	6.62
		B	703	6919	0.58	7.97
	Gervai & Csányi (1985)		253	1334	0.78	16.21
Reduced matrix	Royce, Poley & Yeudall (1973)	A	153	5083	0.69	15.03
		B	91	3337	0.65	20.88
	Gervai & Csányi (1985)		66	897	0.82	12.12

Reanalysis of the data by Royce et al (1973)

Three factors with eigenvalues greater than unity appeared, the VSS index also reached its maximum for the three-factor solution, but the PA method indicated four factors. Although a simulation study by Zwick & Velicer (1986) have found that the PA method is the most accurate in principal component analysis, it is not so in factor analysis (Crawford & Koopman, 1973). Revelle & Rocklin (1979) have also observed that the Montanelli & Humphreys's (1976) procedure based exactly on its logic may show significant overestimation if

communalities and factoring adequacy are low, as it was the case in this study. Additionally, there is a strong ground to discard poorly defined factors retained by the PA method (Zwick & Velicer, 1986). Thus, three factors were extracted.

The rotated factor pattern is presented in Table 2. The first factor is rather easy to interpret, as it is made of the latency to enter the swim way (40), the latency to enter an opaque pipe from an open box (29), the latency to traverse the swim way (41), and has also minor loadings by cell urination (25) and the latency to descend from a 34-inch-high platform (20). Thus, it is likely to reflect a motivation to escape and fearfulness. The second factor is also easily interpretable and, in fact, it closely corresponds to the Motor Discharge factor identified by Royce *et al* (1973). Thus, the first two factors could really represent the Fear-Avoidance and Activity-Exploration, as hypothesized.

Table 2. Varimax-rotated factor loadings: Royce, Poley & Yeudall (1973) data; ** salient loadings (> 0.5); * lower but interpretable loadings (0.3-0.5)

Variables	Factor 1	Factor 2	Factor 3
Open field latency (10)	-.06	.64**	.06
Open field activity (11)	.00	-.79**	.12
Open field penetration (12)	-.10	-.57**	-.09
Straightway latency (15)	-.05	.39*	.32*
Straightway activity (16)	-.09	-.48*	-.13
Latency to leave the platform, pole (19)	.02	.25	.63**
Latency to descend the platform, pole (20)	.42*	.16	.31*
Defecation, pole (21)	.12	.06	.83**
Urination, cell (25)	.47*	-.01	-.06
Hole defecation (27)	.19	.02	.27
Pipe entrance, trial 1 (29)	.63**	.03	-.01
Pipe emergence, trials 2, 3, 4 (32)	.06	-.01	.59**
Underwater swimming, entrance (40)	.76**	-.00	.15
Underwater swimming, latency to traverse (41)	.57**	.02	.27
Eigenvalue	2.61	1.67	1.18
Variance accounted for (%)	18.65	11.94	8.40

The third factor, explaining 8% of variance, is difficult to interpret as it is composed of pole defecation (21), the latency to leave the elevated platform (pole) (19), the latency to emerge from an opaque pipe into the goal-box with several food pellets on trials 2, 3 and 4 (when the animal has already learned that food may be found there) (32), and has also minor loading by (also elevated) straightway latency

(15) and the latency to descend the platform (pole) (20). Although it seems to represent an unusual admixture of fear of an elevated platform and food motivation, it cannot be simply neglected.

However, an inherent two-dimensionality of the data was revealed when 4 (indicated by the PA technique; also a small elbow appeared on the scree plot after this factor) or 5 factors were extracted and submitted to the Wherry (1984) hierarchical rotation procedure. Two clear second-order factors emerged which were almost identical in terms of factor loadings to the above Factor 1 and Factor 2 (Tucker congruence coefficients = 0.96 and 0.83, respectively; Pearson correlation coefficients = 0.95 and 0.91, respectively).

Reanalysis of the data of Gervai & Csányi (1985)

Twelve behavioral variables were factor-analyzed (all variables with multiple $R^2 > 0.5$ had also the KMO > 0.5). Two factors with eigenvalues greater than unity appeared (Table 3), and both VSS and PA technique also revealed two factors. However, the scree-test indicated only one factor and in oblique rotations the factors were correlated, even though their pattern was virtually identical to the Varimax. Two factors were retained as indicated by the more reliable PA and VSS approaches (Revelle & Rocklin, 1979; Zwick & Velicer, 1986). Additionally, the scree test applied in a separate analysis of only marker variables (loadings > 0.7) clearly indicated two factors. These two factors were replicable (see below) and the correlation between them may have been caused by the large number of variables loading on the first factor and small number of variables uniquely identifying the second factor.

The first factor has salient loadings by the frequency of approach to the novel object (a rotating disk) (APF), the time spent near it (APD), latency to emerge from a shelter (in fact, a start-box, EML), air-gulping in the novel object test (AAG), air-gulping latency in a novel environment (AGL), the time spent freezing in a restricted environment (a white plastic dish) (FRD). The first factor is also loaded to a lesser degree by air-gulping duration (RAG) and freezing frequency (FRF) in a restricted space and air-gulping in a novel environment (A-G) (Table 3). Hence, it could be interpreted in terms of exploratory behavior and activity. The second factor has major loadings by freezing (FRZ), escape (ESC), air-gulping (A-G) in a novel environment and air-gulping in the restricted space (RAG). It also has minor loadings by air-gulping in the novel object test (AAG) and freezing in the restricted

space (FRD and FRF). Thus, the second factor may reflect fear motivation and the tendency to escape. That air-gulping contributed to the fear factor, especially in a potentially dangerous novel environment, would be adaptive. That is, a fish overtly swimming near the surface in presence of a dangerous stimuli will expose itself to a high risk. The fact that freezing was related to both factors agrees with the earlier evidence (Gerlai & Hogan, 1992; Budaev, 1997b) that this behavior may reflect both excessive fear and/or a mere inactivity or a relaxed state. Thus, the data obtained by Gervai & Csányi (1985) may also indicate the presence of the two major dimensions.

This two-factor pattern is almost identical to that obtained in the guppy, *Poecilia reticulata* (Budaev, 1997b). The factor similarity coefficients are remarkably large for both factors (Table 4). Thus, the factors are replicable, even in spite of differences in species ecology and environmental conditions during testing.

Table 3. Varimax-rotated factor loadings from data of Gervai & Csányi (1985). ** salient loadings ($p > 0.5$); * lower but interpretable loadings ($p = 0.3$-0.5).

Variables	Variable Code	Factor 1	Factor 2
Freezing duration, restricted space	FRD (1)	-0.56**	-0.39*
Air-gulping, restricted space	RAG (2)	0.48*	0.60**
Freezing frequency, restricted space	FRF (3)	-0.45*	-0.31*
Novel object approach frequency	APF (5)	0.81**	0.19
Air-gulping, novel object approach	AAG (6)	0.63**	0.47*
Novel object approach duration	APD (7)	0.77**	0.14
Latency to emerge from shelter, novel env.	EML (8)	-0.75**	-0.28
Air-gulping latency in a novel environment	AGL (11)	-0.61**	-0.16
Escape attempts in a novel environment	ESC (12)	0.13	0.73**
Swimming in a novel environment	SWI (13)	0.33*	0.25
Freezing in a novel environment	FRZ (21)	-0.19	-0.83**
Air-gulping in a novel environment	A-G (22)	0.38*	0.70**
Eigenvalue		5.37	1.03
Variance accounted for (%)		44.79	8.62

Table 4. Comparison of the two temperament factors identified in the paradise fish (Gervai & Csányi, 1985) and guppy (Budaev, 1997b); *, KHB mean solution cosine.

Factor of temperament	Factor similarity coefficient			
	Ahmavaara	Tucker	Pearson	KHB
Activity-Exploration	0.90	0.90	0.90	0.95
Fear-Avoidance	0.90	0.89	0.89	0.95 (0.94*)

DISCUSSION

In this paper, the mice data of Royce, Poley & Yeudall (1973) and the paradise fish data of Gervai & Csányi (1985) were reanalyzed. By eliminating uncorrelated variables it was possible to achieve much simpler factor solutions than in the original studies. The present results indicate the existence of two general dimensions of temperament in such diverse species, being Activity-Exploration and Fear-Avoidance. These factors were perfectly replicable across studies involving two fish species with different ecologys, even though the testing environments were obviously not identical. Of course, this does not mean that these are the only dimensions of temperament. Additional factors may appear if different tests and variables were used, as well as if not all weakly correlated variables were excluded from the analysis. None the less, the present analysis indicates that Activity-Exploration and Fear-Avoidance tend to be the most general, stable and replicable factors.

Finally, it is curious to note that a similar reduction of an initially very complicated factor structure occurs in the area of human personality studies. For example, Cattell (1973) identified as many as sixteen basic dimensions of personality. However, several recent studies failed to establish any replicability of the Cattell's 16PF. No one has been able to identify more than seven factors in the scales that were the basis of the whole system, and even these provided clear indication of the Extraversion and Neuroticism (Barrett & Kline, 1980; McKenzie, 1988; Saville & Blinkhorn, 1981) as well as the three other dimensions of the Big Five model of personality (see Digman, 1990 for a review).

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REFERENCES

Armstrong, J.S., & Soelberg, P. (1968). On the interpretation of factor analysis. *Psychological Bulletin, 70,* 361-364.

Barrett, P. (1986). Factor comparison: An examination of three methods. *Personality and Individual Differences, 7,* 327-340.

Barrett, P., & Kline, P. (1980). The location of superfactors P, E, and N within an unexplored factor space. *Personality and Individual Differences, 1,* 239-247.

Budaev, S.V. (1997a). The dimensions of personality in animals: The comparative and evolutionary framework. In M. Taborsky & B. Taborsky (Eds.) *Advances in Ethology,* Contributions to XXV International Ethological Conference, Vienna, Austria, 20-27 August 1997 (vol. 32, p. 90). Berlin: Blackwell Wissenschafts-Verlag (Abstract).

Budaev, S.V. (1997b). "Personality" in the guppy (*Poecilia reticulata*): A correlational study of exploratory behavior and social tendency. *Journal of Comparative Psychology, 111,* 399-411.

Cattell, R.B. (1973). *Personality and mood by questionnaire.* San Francisco: Jossey-Bass.

Cattell, R.B., & Korth, B. (1973). The isolation of temperament dimensions in dogs. *Behavioural Biology, 9,* 15-30.

Clark, A.B., & Ehlinger, T.J. (1987). Pattern and adaptation in individual behavioral differences. In P.P.G. Bateson & P.H. Klopfer (Eds.) *Perspectives in ethology* (vol. 7, pp. 1-47). New York: Plenum Press.

Crawford, C.B., & Koopman, P. (1973). A note on Horn's test for the number of factors in factor analysis. *Multivariate Behavioral Research, 8,* 117-125.

Digman, J.M. (1990). Personality structure: Emergence of the five-factor model. *Annual Review of Psychology, 41,* 417-440.

Dziuban, C.D., & Shirkey, E.S. (1974). When is a correlation matrix appropriate for factor analysis? Some decision rules. *Psychological Bulletin, 81,* 358-361.

Eysenck, H.J., & Eysenck, M.W. (1985). *Personality and individual differences. A natural science approach.* New York: Plenum Press.

Gerlai, R., & Csányi, V. (1990). Genotype-environment interaction and the correlation structure of behavioral elements in paradise fish (*Macropodus opercularis*). *Physiology and Behavior, 47,* 343-356.

Gerlai R., & Hogan J.A. (1992). Learning to find the opponent: an ethological analysis of the behavior of paradise fish (*Macropodus opercularis*) in intra- and interspecific encounter. *Journal of Comparative Psychology, 106,* 306-315.

Gervai, J., & Csányi, V. (1985). Behavior-genetic analysis of the paradise fish, *Macropodus opercularis.* I. Characterization of the behavioral responses of inbred strains in novel environments: A factor analysis. *Behavior Genetics, 15,* 503-519.

Guilford, J.P. (1977). The invariance problem in factor analysis. *Educational and Psychological Measurement, 37,* 11-19.

Horn, J.L. (1967). On subjectivity in factor analysis. *Educational and Psychological Measurement, 27,* 535-538.

Humphreys, L.G., Ilgen, D., McGrath, D., & Montanelli, R. (1969). Capitalization on chance in rotation of factors. *Educational and Psychological Measurement, 29,* 259-271.

McKenzie, J. (1988). Three superfactors in the 16PF and their relation to Eysenck's P, E, and N. *Personality and Individual Differences, 9,* 843-850.

Montanelli, R.G.Jr., & Humphreys, L.G. (1976). Latent roots of random data correlation matrices with squared multiple correlations on the diagonal: A Monte Carlo study. *Psychometrika, 41,* 341-348.

Revelle, W., & Rocklin, T. (1979). Very simple structure: An alternative procedure for estimating the optimal number of interpretable factors. *Multivariate Behavioral Research, 14,* 403-414.

Royce, J.R. (1977). On the construct validity of open-field measures. *Psychological Bulletin, 84,* 1098-1106.

Royce, J.R., Poley, W., & Yeudall, L.T. (1973). Behavior genetic analysis of mouse emotionality: I. Factor analysis. *Journal of Comparative and Physiological Psychology, 83,* 36-47.

Saville, P. & Blinkhorn, S. 1981. Reliability, homogeneity, and the construct validity of 16PF. *Personality and Individual Differences, 2,* 325-333.

Stevenson-Hinde, J. (1983). Individual characteristics: a statement of the problem. Consistency over time. Predictability across situations. In R.H. Hinde (Ed.) *Primate social relationships: An integrated approach* (pp. 28-34). Oxford: Blackwell.

Walsh, R.N., & Cummins, R.A. (1976). The open-field test: a critical review. *Psychological Bulletin, 83,* 482-504.

Wherry, R.J. (1984). *Contributions to correlational analysis.* New York: Academic Press.

Wilson, D.S., Clark, A.B., Coleman, K., & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends in Ecology and Evolution, 9,* 442-446.

Wright, S.P. (1992). Adjusted P-values and simultaneous inference. *Biometrics, 48,* 1005-1013.

Zwick, W.R., & Velicer W.F. (1986). Comparison of five rules for determining the number of components to retain. *Psychological Bulletin, 99,* 432-442.

STARTLE - FREEZE BEHAVIOUR
IN WEANED PIGS

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ABSTRACT: Pigs may express a startle response and then freeze after they have heard an auditory stimulus. The objective of this study was to induce startle-freeze behaviour, describe it and to seek potential variables that might influence it. A startle-freeze response lasting 1 to 12 seconds was produced in 36 pigs 5-6 weeks old penned in 12 groups (3 pigs per group), using a cymbal (26 cm radius) to produce a sound of 110 dB intensity. This was repeated at 4 minute intervals for 8 stimuli over 28 minutes. The duration of the startle-freeze response decreased over presentations and all pigs had ceased to respond by the seventh stimulus. The frequencies of social interaction, ingestion and lying or sitting behaviours before freezing decreased after the freeze period, and standing or walking increased. The behaviours shown before and after immobilisation were not independent ($\chi^2_4 = 101.9$, $p < 0.001$). The social status of each group was determined from videotape records. The dominance rank of the pig was significantly related to the onset of immobilization; the most dominant pigs responded to the noise first, often 1 to 2 seconds ahead of lower ranked pigs ($\chi^2_6 = 15.74$, $p < 0.05$). In conclusion, pigs show a clear startle-freeze response to a novel auditory stimulus, they habituate rapidly and the onset of startle-freeze behaviour depends upon their social status.

The first protective response given to sudden sound is a startle or "auditory startle" response. Any general massive body flexion in animals in response to sudden intense stimulation is referred to as a startle. The "auditory startle" is specifically in response to a sudden sound (Salzen, 1979). Marks (1987) referred to it as a momentary fear of a sudden stimulus. Inhibition, freezing and crouching follow

auditory startle and are responses to sounds intermediate between those that will elicit the full startle and the orientating reflexes (Salzen, 1979).

Ratner (1967) observed that animals freeze and become temporarily immobile when a novel or threatening stimulus is presented. There is evidence that this freeze response is a type of fear reaction to a novel stimulus (Archer, 1979). Marks (1987) referred to freezing as attentive immobility when an alerted individual remains motionless and monitors the source of danger, ready for flight or fight in an instant. Archer (1979) showed that when a bell was sounded in an open field situation, chickens froze and did not emit distress calls.

Fear shows a diverse group of behaviour patterns including those leading to avoidance of a stimulus and immobility responses (Hinde, 1970, pp 349-351). Thus, flight and immobility are broad behavioural categories induced by novel and potentially fear-inducing situations; both categories include several different types of response.

The types of immobility which occur in fear-inducing conditions are overlapping (Archer, 1979). The first type is freezing which is a relatively short-lived period of immobility shown by many species of animal. It may be accompanied by a crouching posture. There is a further type of immobility, tonic immobility which occurs in a wide range of vertebrate and invertebrate species in response to physical restraint (Archer, 1979).

It is important to differentiate between freezing immobility (often called immobility) and tonic immobility. Gallup (1974) reviewed animal hypnosis or tonic immobility, and pointed out that some form of physical restraint is usually necessary for the tonic immobility responses. However, Marks (1987) quoted experimental work which indicated tonic immobility could be reliably elicited by sudden noise, or being thrust into new surroundings or by suddenly turning an animal on its back.

Tonic immobility is longer-lived than freezing immobility and the animal remains responsive to external stimulation. It is brought about by the tonic action of both extensor and flexor muscles involved in struggling, and the animal's attempts to escape (Archer, 1979; Salzen, 1979).

Both tonic immobility and freezing are defensive reactions that begin abruptly in the face of danger (Marks, 1987). Freezing is preparatory or an intention movement of flight while tonic immobility is a terminating reaction to being caught. This might explain why freezing is more common than tonic immobility. Also during freezing, the animal is in the alert posture typical for that species, whereas tonic

immobility often leaves the animal in unusual postures (Marks, 1987).

Ratner (1967) gave a clear account of the sequence of stimuli and responses associated with decreasing defensive distance between the position of the threatening stimulus and the animal. First the animal freezes to a typical visual or auditory stimulus which is at a distance. As the distance between the threatening stimulus and the animal decreases, the animal tries to escape, or flee and finally reaches tonic immobility. Any stimulus that functions as a threatening stimulus elicits a sequence of responses as a function of the distance between the stimulus and the animal.

These responses appear early in ontogeny. Borchelt and Ratner (1973) described the ontogeny of both freezing and tonic immobility in the bobwhite quail (*Colinus virginianus*) in response to handling and the visual presence of the experimenter. Freezing was more common than tonic immobility at 9-10 days and by 15 days the first strong responses of tonic immobility appeared with a median duration of 60 seconds and occurred with a mean duration of 10 seconds.

In the rat Bolles and Wood (1964) observed freezing to a sudden noise at 23 days of age and Fox (1970) saw freezing in the cat following an auditory stimulus from 13 days. The development of inhibition, freezing and crouching follows a standard pattern in altricial birds and involves developing responsiveness first to auditory and then to visual stimulation (Salzen, 1979). Salzen (1979) concluded that the early appearance of inhibition and freezing to auditory stimuli seemed to be associated with early auditory responsiveness and unlocalised stimulation. He also commented that in precocial mammals inhibition and crouching develop with the startle response and this is evident if there is a disturbing stimulus and the parent is absent.

The trend of recent work has been to use the tonic immobility response as an indication of fear which might be induced in domestic hens by transport (Scott *et al.*, 1998) high stocking density (Andrews et al., 1998), group size (Bilcik *et al.*, 1998) and forms of restraint such as shackling and diverse hooding devices (Jones *et al.*, 1998). However, there are no comments in any of these studies on the presence or absence of the initial startle-freeze response. Also, most of the recent work has been done with domestic hens.

One paper (Dawson and Revens, 1946) described an alarm response in pigs in which an electric sparking device (which produced a distinct, though not loud, hissing and crackling sound) was used to scare pigs away from the feed trough.

Animals can habituate to a variety of stimuli and habituation of

simple and complex defensive responses is very similar across species. Habituation refers to the decrement in response as discrete stimuli are repeated and is largely independent of motivational states, biological cycles or age (Marks, 1987). Hinde (1970, pp 577-579) commented that sometimes the difference between habituation and extinction is difficult to define.

Intensively housed pigs startle and freeze when a strange, often loud, noise occurs, and they take a short time to begin moving again (Blackshaw, pers obs). We found no discussion in the scientific literature of this response in pigs.

The aims of this experiment were to document the startle-freeze behaviour in young weaned pigs, in response to a loud noise, to determine how many presentations of the stimulus were needed before the pigs no longer responded and to explore the possibility that position in the dominance hierarchy might influence freezing behaviour.

METHOD

Subjects

Three blocks of 4 pens (1.2 m x 1.2 m) each containing 3 pigs from different litters (PIC Camborough – 15 crosses), 5 to 6 weeks old were tested (n = 36 pigs). The pigs in each pen were visually isolated from the other pens, with wooden boards between adjacent pens. At weaning (28 d of age) pigs from three litters were identified individually and placed in each nursery pen. Time lapse video recorders, filming at 0.83 frames/sec for 24 hours were used to assess the food competition dominance hierarchy.

Procedure

Food competition dominance. Groups of weaned pigs were food restricted; the trough was not refilled the evening before the food competition dominance rank was assessed. The pigs were fed next morning and agonistic behaviour (including fighting, biting, head thrusting, threat, displacement at the feed trough) was recorded on the time lapse video recorder. Each pig was marked so that the initiator and recipient of the behaviours could be identified. Matrices were generated for each group and the pigs were ranked according to the winning of agonistic encounters at the feed station (Beilharz and Cox, 1967; Signoret, Baldwin and Hafez, 1975).

Startle – freeze response.   The startle-freeze response was generated with a 26 cm (radius) cymbal suspended from a wire loop equidistant from the 4 pens. The sound intensity in the centre of the 4 pens was 109 to 110 dB, measured with a "Realistic" sound level meter (Tandy Corporation, Cat. No. 33-2050) which had a range of measurement 50-126 dB and accuracy of ± 2 dB at 114 dB sound level. The sharp sound was tested for repeatability and intensity in the test room. Eight single strikes with a wooden drumstick (noise stimuli) were generated at 4-minute intervals and the response in each pen recorded on videotape (30 frames/sec) using colour cameras with video and audio recording. For viewing, videotapes were played in slow motion (down to 0.8 frames/sec).

Observations

As each pig had been identified and ranked, it was possible from the videotapes to record for each pig:

1. the behaviour immediately before the startle-freeze sequence; lie or sit, stand or walk, feed-with head in the trough, drink (or at the drinker) and social interactions (while lying or standing)
2. the length of the freeze behaviour in seconds
3. the order of on-set in which each pig in the group showed freeze behaviour and the order in which they resumed activity after freezing
4. the behaviour (as above) the pigs resumed after freezing
5. the length of time and number of exposures taken for habituation to the noise.

Analyses

The data set included 36 pigs from 12 replicate pens with each pen including pigs of socially dominant, intermediate and subordinate status. Regression analysis was used to assess freeze period (seconds) time over number of cymbal strikes ($n = 8$). Linear, quadratic and cubic coefficients were calculated. Parametric and non-parametric analyses of social status effects on order of movement after freezing yielded identical conclusions. The chi-square analysis with social status in rows and order of freeze behaviour in columns was assessed using General Linear Models Procedure (SAS, 1988).

RESULTS

The strike on the cymbal produced a pronounced startle-freeze response, which decreased over subsequent presentations. Figure 1 shows the mean startle-freeze duration (seconds) with repeated exposures to the auditory stimulus (n = 8, 4 minutes apart), for 36 pigs. The end of the startle-freeze sequence was marked by movement of the pig's head, which occurred whether the pig was standing, sitting, or lying. The behaviours before and after immobilization were significantly different (χ^2_4 = 101.9, p < 0.001). Freezing, on presentation of the stimulus, disrupted the frequencies of social interaction (51 vs 9), ingestion (50 vs 23) and lying or sitting (137 vs 98), but standing or walking were increased greatly (50 vs 158) after freezing.

Position in the hierarchy did not influence (p > 0.05) individual pig behaviour (lie or sit, stand or walk, ingestion and social interaction) before the sound stimulus, immediately after the freeze behaviour or 10 second later. Also, when rank was not considered, there was no differences in behaviour (p > 0.05) before or immediately after freezing in individual pigs, 10 seconds later.
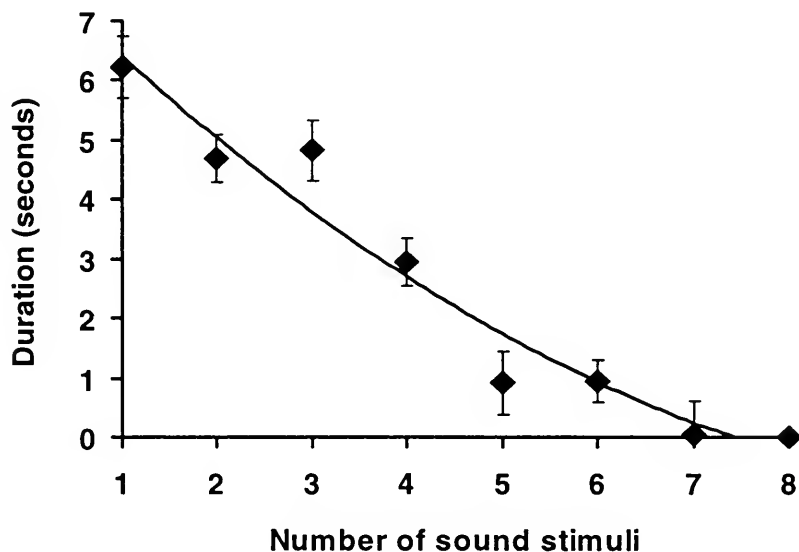

Figure 1. Startle-freeze duration (seconds) with repeated exposures to the sound of a cymbal. Shown is the mean results for 36 pigs. Each auditory stimulus (n = 8) was 4 minutes apart. The regression equation for the cubic effect was: $Y = 6.297 + 0.1129X - 0.375X^2 + 0.034X^3$, ($r^2 = 0.96$).

When individual startle exposures (corresponding to the cymbal strikes) were examined, there was no relationship between the rank of the pig and the behaviour before or immediately after freezing or 10 seconds later.

The latency of onset of freezing was highly related to the position of the pig in the hierarchy (Table 1). The dominant pigs usually responded to the noise stimulus first, this was often 1 to 2 seconds ahead of the lower ranked pigs who were more often last to freeze ($\chi^2_6 = 15.74$, $p < 0.05$). The order of pigs resuming activity directly after freezing was independent of dominance rank and the length of the freeze response was not related to dominance rank.

Table 1. Numbers of observations for pigs of each social status (n=12) and their order of startle-freeze behaviour (first, second or third to freeze or "no response " for pigs in which the behaviour waned) in response to 8 presentations of the auditory stimulus (1 per 4 minutes). The number of freeze behaviours possible was 288 ($\chi^2 = 15.74$, $p<0.05$).

Hierarchy	Order of Freeze Behaviour			
	1	2	3	No response
Dominant	33	13	3	47
Intermediate	38	11	6	40
Subordinate	33	6	16	42
Total	104	30	25	129

Eventually, as habituation occurred, no pigs exhibited freezing behaviour. Figure 2 shows the percentage of pigs no longer responding to each successive presentation of the stimulus. By presentation 5 (after 16 minutes), 67% of the pigs no longer responded and by stimulus 7 (24 minutes) all the pigs had ceased to show a response.

DISCUSSION

A loud auditory stimulus (109-110 dB) produced a clear startle-freeze response in pigs which was repeatable and all pigs tested responded, at least once, to the stimulus. It appeared to be an attentive yet fearful response, similar to that described by Gallup (1974) and Archer (1979). No record could be found in the literature which described this behaviour in pigs, and the only paper which described an
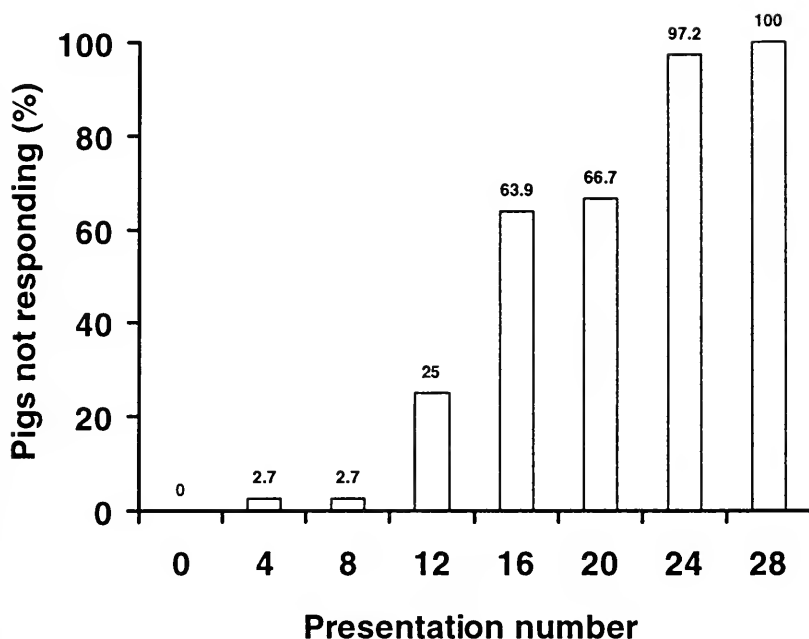
Figure 2. Percentage of pigs (n = 36) which did not respond to the auditory stimulus at each presentation.

alarm response in pigs was that of Dawson and Revens (1946). The sequence of responses in the pig to auditory stimuli did not progress from the startle-freeze response to tonic immobility. The length of freezing was much shorter in the pig (1 to 12 s) than the final response (tonic immobility or death feigning) of many species, to fear. Ewell and Cullen (1981) described tonic immobility in the rabbit (180 to 183 s and 61 to 63 s), Satterlee *et al.* (1993) found that Japanese quail immobilized for 102 to 201 s, and chickens were immobilized for 51 to 154 s (Gallup *et al.,* 1970). The bobwhite quail showed freeze behaviour lasting 10 seconds at 9-10 days which by 15 days progressed to tonic immobility (Borchet and Ratner, 1973).

The domesticated pig's response to a novel sound stimulus, which most likely has an element of fear involved, did not progress to tonic immobility. Pigs have few natural predators in the wild and their response to novel stimuli is often to run away (unless cornered). With this alarm-response strategy, the initial startle and short freeze period perhaps allows the pig to orientate before fleeing if the danger increases.

Why does the top ranking pig freeze first? Perhaps it is evidence of a defense mechanism, which protects the social structure of a group, in which the high status animal is the most important social force. This suggests that there may be an association between alertness and dominance. The dominant pig is the one which others in the group attend to and recognise. Ewbank and Meese (1971) showed this in their experiment in which the high status animal could be removed for up to 25 days and safely returned, whereas low status pigs were attacked severely after only 3 days absence.

The response to the auditory stimulus decreased with progressive exposure. After the seventh presentation of the stimulus no pigs responded. The orientating response waned gradually. This is a normal response to a stimulus, which initially elicits an orientating response and is repeated at intervals. If the stimulus is without consequence, first there is a reduction in those physiological components of the response associated with generalised sensory alerting. This changes to a localised orientating response, which either wanes or becomes an adaptive response and the specific features of the stimulus (in this case noise) which invoked the initial response, tend to be reduced (Hinde, 1970, pp 131-132). The pigs showed this progression of responses, as the stimulus was of no consequence to them and their behaviour patterns were not disrupted.

This study is the first to record the orientating response of startle-freeze behaviour in pigs. The response is easy to elicit and therefore it would be interesting to look at the behaviour in larger group sizes.

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REFERENCES

Andrews, S.M., Omed, H.M. and Phillips, C.J.C. (1998). The effect of a single high stocking density on the behaviour and response to stimuli in broiler chickens. *Poultry Science*, 76, 1655-1660.

Archer, J. (1979). Behavioural aspects of fear. In W. Sluckin (Ed.), *Fear in animals and man* (pp 56-85). NY: Van Nostrand Reinhold Company.

Beilharz, R.G. and Cox, D.F. (1967). Social dominance in swine. *Animal Behaviour, 15,* 117-122.

Bilcik, B., Keeling, L.J. and Newberry, R.C. (1998). Effect of group size on tonic immobility in laying hens. *Behavioural Processes, 43,* 53-59.

Borchelt, P.L. & Ratner, S.C. (1973). Development of freezing and immobility, predator defenses, in the Bobwhite Quail *(Colinus virginianus). Behavioral Biology, 8,* 83-92.

Bolles, R.C. & Woods, P.J. (1964). The ontogeny of behaviour in the albino rat. *Animal Behaviour, 12,* 427-441.

Dawson, W.M. & Reeves, R.L. (1946). Varying susceptibility in pigs to alarm. *Comparative Psychology, 39,* 297-305.

Ewbank, R. and Meese, G.B. (1971). Aggressive behaviour in groups of domesticated pigs on removal and return of individuals. *Animal Production, 13,* 685-693.

Ewell, A.H. and Cullen, J.M. (1981). Tonic immobility as a predator-defense in the rabbit (Oryctolagus cuniculus). *Behavioral and Neural Biology, 31,* 483-489.

Fox, M.W. (1970). Reflex development and behavioral organization. In W.A. Himwick (Ed.), *Developmental Neurobiology* (pp 553-580). Sprinfield, Ill.: Thomas.

Gallup, G.G. (1974). Animal hypnosis: Factual status of a fictional concept. *Psychological Bulletin, 81,* 836-853.

Gallup, G.G. Jr., Nash, R.F., Potter, R.J. and Donegan, N.H. (1970). Effect of varying conditions of fear on immobility reactions in domestic chickens (Gallus gallus). *Journal of Comparative and Physiological Psychology, 73,* 442-445

Hinde, R.A. (1970). *Animal behaviour. A synthesis of ethology and comparative psychology,* (2nd ed.). McGraw-Hill Inc.

Jones, R.B., Hagerdorn, T.K. and Satterlee, D.G. (1998). Adoption of immobility by shackled broiler chickens: effects of light intensity and diverse hooding devices. *Applied Animal Behaviour Science, 55,* 327-335.

Marks, I.M. (1987). *Fears, phobias, and rituals* (pp 60-69). NY: Oxford University Press.

Ratner, S.C. (1967). Comparative aspects of hypnosis. In J.E. Gordon (Ed.), *Handbook of clinical and experimental hypnosis* (pp 550-587). NY: The Macmillan Company.

Salzen, E.A. (1979). The ontogeny of fear in animals. In W. Sluckin (Ed.), *Fear in animals and man* (pp 125-163). NY: Van Nostrand Reinhold Company.

SAS Institute Inc. (1988). *SAS/STAT Users Guide,* Release 6.03 Edition (pp 1028). Cary, N.C.: SAS Institute Inc.

Satterlee, D.G., Jones, R.B. and Ryder, F.H. (1993). Short-latency stressor effects on tonic immobility fear reactions of Japanese Quail divergently selected for adrenocortical responsiveness to immobilization. *Poultry Science, 72,* 1132-1136.

Scott, G.B., Connell, B.J. and Lambe, N.R. (1998). The fear levels after transport of hens from cages and a free-range system. *Poultry Science, 77,* 62-66.

Signoret, J.P., Baldwin, B.A. & Hafez, E.Z.E. (1975). *The behaviour of domestic animals,* (3rd Ed.) (pp 295-329). London: Baillière Tindall.

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